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A NEOSELACHIAN SHARK FROM THE NON-MARINE WESSEX FORMATION (WEALDEN GROUP: EARLY CRETACEOUS, BARREMIAN) OF THE ISLE OF WIGHT, SOUTHERN ENGLAND

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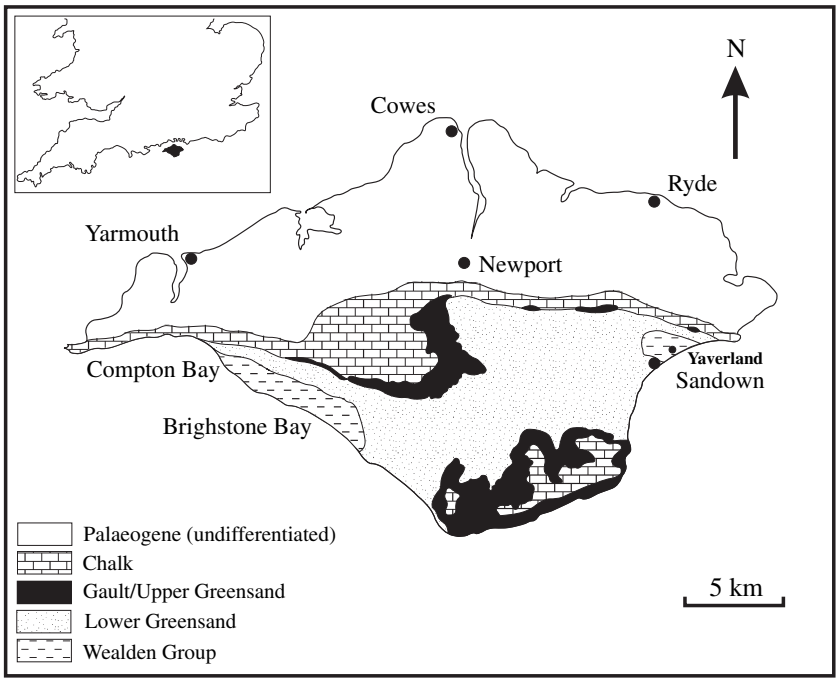
Abstract: Bulk screening of Early Cretaceous (Barremian) Wessex Formation strata exposed on the south-east coast of the Isle of Wight, southern England, has resulted in the recovery of neoselachian shark teeth referred to the scyliorhinid *Palaeoscyllium*. These are the first neoselachian remains from the British Wealden Group and represent the geologically oldest neoselachian yet recovered from a freshwater deposit. This is also the only known example of a non-marine occurrence of a member of the Scyliorhinidae.

Key words: Britain, Cretaceous, Neoselachii, *Palaeoscyllium*, shark, Wealden.

HYBODONT shark teeth and other remains are common within the non-marine facies of the British Wealden Group, occurring often in high concentrations in winnowed bone beds. Despite this high abundance, only one study has attempted to describe the shark tooth fauna (Patterson 1966), with other work (e.g. Woodward 1916, 1919) dealing only with larger, macroscopic remains. Since that time, the microvertebrate fauna, including the sharks, of the Wealden Group has received scant attention, in part due to cessation of work to recover mammalian fossils (Clemens and Lees 1971) and perhaps to some degree due to difficulties associated with extracting vertebrate remains from sideritic bone beds. The study by Patterson (1966) did not include material from the Wessex Formation of the Isle of Wight, and whilst macroscopic shark remains have been recorded from the island (e.g. Egerton 1845), the microvertebrate fauna has largely remained undescribed, with most records of shark material being within species lists without figures (e.g. Freeman 1975). From the Wessex Formation exposed on the south-west coast of the island, Butler and Ford (1975) reported teeth of *Hybodus* (now probably *Egertonodus*) sp. and teeth and spines of *Lonchiodon* (misspelling of *Lonchidion*) spp., whilst Freeman (1975) reported *Lonchidion striatum* Patterson, 1966, '*Hybodus*' *basanus* Egerton, 1845, and *Hylaeobatis ornata* (probably assignable, like material from the Vectis Formation, to *Vectiselachos ornatus* Woodward, 1889; Rees and Underwood 2002). The latter study also recorded more abundant shark remains from the overlying Vectis Formation including '*Hybodus*' *parvidens* Woodward, 1916, '*H*'. *brevicostatus* Patterson, 1966, '*H*'. spp., '*Hylaeobatis*' *ornata*, '*Hy*'. sp. and *Lonchidion* spp. Stewart (1978, pp. 55–57) also reported a diverse hybodont fauna, but it appears that the majority of the taxa listed were obtained from the Vectis Formation. More recently '*Hybodus*' *parvidens*, *Lonchidion breve* Patterson, 1966, *L. striatum* Patterson, 1966 [recorded as *Lissodus breve* (Patterson, 1966) and *L. striatus* (Patterson, 1966)] and other indeterminate hybodont material were recovered from the site that yielded the allosauroid dinosaur *Neovenator* Hutt *et al.*, 1996 (Evans *et al.* 2004). Hybodont fin spines are also reportedly common at the boundary between the Wessex Formation and the overlying Vectis Formation in the vicinity of Cowleaze Chine (NGR SZ 443801; D. Martill, pers. comm. 2004). The discovery of rich microvertebrate-bearing horizons within the Early Cretaceous (Berriasian) Purbeck Limestone Formation in Dorset, southern England (e.g. Ensom *et al.* 1994), contrasted strongly with the apparent scarcity of Wessex Formation microvertebrate fossils and prompted comprehensive bulk screening of Wessex Formation strata (Sweetman 2004, in press and work in progress). This has resulted in the recovery of a large number of hybodont shark teeth and other microvertebrate remains, including the neoselachian teeth described here.



TEXT-FIG. 1. Outline geological and location maps of the Isle of Wight.

GEOLOGY

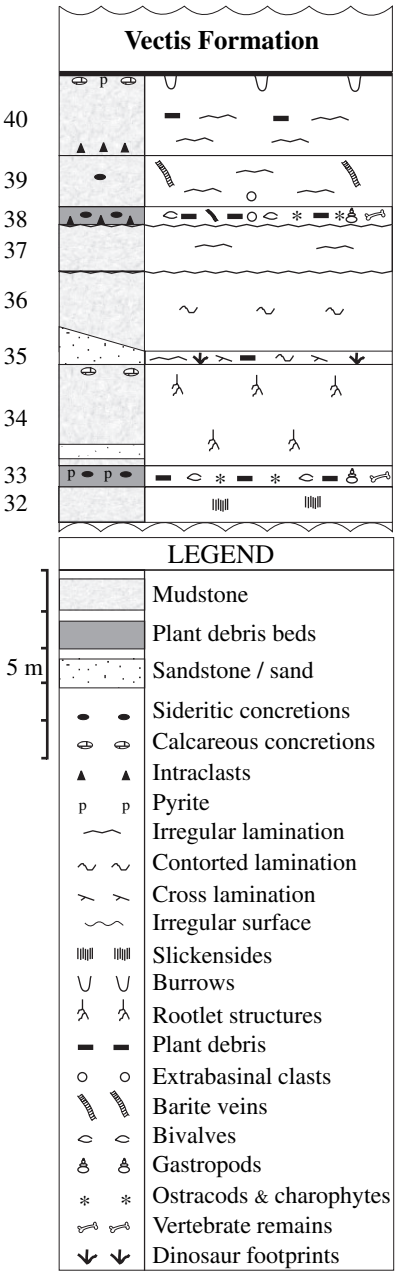
The Wealden Group of the Isle of Wight comprises two formations: the essentially fluvio-lacustrine Wessex Formation overlain by the largely lagoonal Vectis Formation. Both formations are very well exposed in cliff sections on the south-west and south-east coasts of the island (Text-fig. 1) where the total thickness of exposed strata is estimated to be about 250 m (Stewart 1978, 1981). However, borehole data (Falcon and Kent 1960) proved a total thickness of 592 m for the Isle of Wight Wealden Group as a whole. Estimates of the thickness of exposed Wessex Formation strata vary due to the difficulty in ascertaining the throw on some faults, and problematic correlation resulting from the laterally discontinuous nature of many of the beds, but Stewart (1978, 1981) estimated the thickness to be about 180 m. The Wessex Formation is composed of interbedded non-marine facies including varicoloured overbank mudstones, crevasse splay deposits, fluvial sandstones and calcrete conglomerates, and beds formerly called lignites (White 1921) but now, in view of palaeoenvironmental and sedimentological considerations, termed plant debris beds (*sensu* Oldham 1976). A Barremian age has been established for these strata (Allen and Wimbledon 1991; Feist *et al.* 1995), with the Hauterivian/Barremian boundary lying close to the base of the exposed Wessex Formation (Hughes and McDougall 1990). The fluvial-associated Wessex Formation was deposited on a low-gradient, near-coast floodplain by a high-sinuosity river system flowing from west to east within a confined, fault-bounded valley (Martill and Naish 2001 and references therein; Underhill 2002). The overlying, largely lagoonal strata of the Vectis Formation are of Late Barremian – Early Aptian age (e.g. Robinson and Hesselbo 2004) and in contrast to the Wessex Formation a number of horizons, particularly in the upper part of the Shepherd's Chine Member, provide evidence for raised salinities at times (e.g. Stewart *et al.* 1991; Radley and Barker 1997, 1998).

Despite year-round high precipitation rates, seasonal aridity resulting from high summer evaporation (Haywood *et al.* 2004; but for an alternative interpretation of the cause of aridity, see Allen 1998) rendered vegetation on the Wessex floodplain susceptible to wildfires and the denuded landscape immediately thereafter vulnerable to erosion by storm waters (Insole and Hutt 1994). The plant debris beds, which make up only about 1 per cent of the Wessex Formation succession, but from which the majority of vertebrate fossils are recovered, represent deposits derived from such local fire and storm events (Insole and Hutt 1994). The fossil assemblage in these beds is therefore also likely to have been of local origin. The large reptile fauna is relatively well known and while most of the material is fragmentary, occasional articulated skeletons have been recovered (Martill and Naish 2001 and references therein). The microvertebrate fauna recovered from the plant debris beds comprises essentially disarticulated (but occasionally associated) remains of dinosaurs, crocodiles, turtles, pterosaurs, lepidosaurs, lissamphibians, mammals, and chondrichthyan and osteichthyan fishes (Evans *et al.* 2004; Sweetman 2004, in press).

A total of 25 fossiliferous horizons have been sampled but whereas all have yielded hybodont remains, only bed 38 (Radley 1994) at Yaverland on the south-east coast (Text-figs 1–2) has yielded neoselachian teeth. Bed 38 is lithologically a typical Wessex Formation plant debris bed (see Stewart 1978, 1981; Insole and Hutt 1994) occurring about 4 m below the top of the Wessex Formation exposed at NGR SZ 617852 (Text-fig. 2). It contains a variably developed basal conglomeratic lag comprising reworked calcrete nodules, other intraformational clasts, and plant and vertebrate remains. Above is a grey, silty clay containing locally abundant, poorly sorted plant material including fusain, small siderite concretions, pyrite nodules, unionoid bivalves and vertebrate remains. The basal boundary of the bed is sharp and undulatory, and fills what was probably a partly eroded, dinosaur-trampled surface. The top of the bed is indistinct, gradually passing upward into the overlying mudstone lithology. The bed is up to about 1·25 m thick but in some exposures appears to be as little as 0·5 m thick. The precise age of bed 38 is poorly constrained. However, Feist *et al.* (1995) placed the Early Barremian/Late Barremian boundary at the base of the overlying Vectis Formation, indicating that bed 38 is probably of latest Early Barremian age. Charophytes recovered from bed 38 during this study may provide better dating in due course (Feist *et al.* 1995; M. Feist, pers. comm. 2004 to SCS).

METHODS

Bed 38 is usually poorly exposed due to slumping of the cliff section and the accumulation of beach deposits which obscure foreshore exposures. However, samples totalling about 150 kg dry weight were collected. Dried samples were sieved using a bulk screening machine (Ward 1981) modified for use with recirculated water and incorporating a sieve with 330-μm mesh. After processing, coarse material (> 2·8 mm) was removed. Plant material in the < 2·8-mm fraction was removed hydromechanically and, when dry, the remaining residue was graded and picked under a binocular microscope. The presence of potentially important calcareous invertebrate and plant fossils prevented further processing using acids and high-density liquids. As a result, and in view of the relatively large volume of residue, composed primarily of siderite particles, time constraints prevented any attempt to recover fossils from the < 500-μm sieve fraction. In addition, samples totalling about 275 kg dry weight were taken by a private collector, Mr Brian Gasson, who processed them using hand-held sieves, the finest of which had a mesh size of 500 μm. The former samples yielded three neoselachian teeth (Text-fig. 3A–H) and the latter two neoselachian tooth crowns (Text-fig. 3I–L) and three



TEXT-FIG. 2. Schematic lithological log of the upper part of the Wessex Formation exposed at Yaverland between NGR SZ 6162 8516 and 6182 8525 (based on Radley 1994, fig. 2, with minor amendments and additions).

fragments (not figured). Digital images of the specimens were obtained using a scanning electron microscope and measurements were taken digitally using associated software (SemAfore version 4.00, Insinööritoimisto J. Rimppi Oy).

Institutional abbreviation. Specimens described here are accessioned in the collections of the Natural History Museum, London, BMNH.

SYSTEMATIC PALAEONTOLOGY

Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Order CARCHARHINIFORMES Compagno, 1977
Family SCYLIORHINIDAE Gill, 1862

Genus PALAEOSCYLLIUM Wagner, 1857, *non* Marck, 1863

Type species. *Palaeoscyllium formosum* Wagner, 1857, from the marine Upper Jurassic of Germany.

Palaeoscyllium aff. *formosum* Wagner, 1857
Text-figure 3

Horizon and locality. Bed 38 (Radley 1994), about 4 m below the top of the Wessex Formation exposed at Yaverland on the south-east coast of the Isle of Wight, southern England, NGR SZ 61693 85223 (Text-figs 1–2).

Material. Five isolated teeth: BMNH P 66293–66295, 66298, 66299.

Description. All five teeth are small, between about 0·75 mm (BMNH P 66923) and 1·25 mm (BMNH P 66299) high (measured along the central line of the labial surface of the principal cusp). Presumed tooth positions are from comparisons with heterodonty in modern scyliorhinids figured by Herman *et al.* (1990) and the study of modern dentitions by CJU. The teeth comprise: BMNH P 66293, a well-preserved tooth from a presumed upper anterior file (Text-fig. 3A–C); BMNH P 66294, a well-preserved, presumed lateral tooth, lacking only the anterior lateral accessory cusp (Text-fig. 3D–F); BMNH P 66295, a partial, presumed anterior tooth (Text-fig. 3G–H); BMNH P 66298, a well-preserved, presumed lower anterior tooth crown, lacking only one accessory cusp (Text-fig. 3I–J); and BMNH P 66299, a well-preserved tooth crown from a presumed lower anterior file (Text-fig. 3K–L).

The crowns (of the more complete teeth) are higher than wide, comprising a slender main cusp and a pair of sharply pointed accessory cusps, reaching less than half of the height of the main cusp. BMNH P 66298 and 66299 also possess minute cusplets at the base of one only of the accessory cusps (Text-fig. 3I–L). All cusps are oval in cross-section and have a cutting edge reaching to the apex. The labial face of the crown is ornamented by a number of straight ridges, extending from the close to the tips of the cusps to the base of the crown. In BMNH P 66293, 66294 and 66295 these ridges bifurcate basally within the lower third of the crown but bifurcation is absent in BMNH P 26698 and 26699. In all specimens labial ridges become rather swollen basally. The lingual faces of all cusps are ornamented with fine, somewhat sinuous, longitudinal ridges that do not extend to the tips of the cusps but which do extend to the base except in BMNH P 66294 (Text-fig. 3D). The root is relatively low and overhung by the crown on the labial side. A thin layer of enameloid coats the uppermost parts of the root. The basal face of the root is only slightly convex and strongly V-shaped in profile. The lingual apex of the root is swollen, and the ends of the root lobes are strongly flared, giving the root a lobate profile. There is a well-developed foramen at the lingual end of the root, and in one tooth, BMNH P 66293, this is enlarged to form a groove (Text-fig. 3A). A small, centrally situated foramen is present on the lingual root face below the broken accessory cusp seen in BMNH P 66294 (Text-fig. 3D) and a more pronounced, elongate foramen is present in a similar position below the accessory cusp preserved in BMNH P 66293 (Text-fig. 3A).

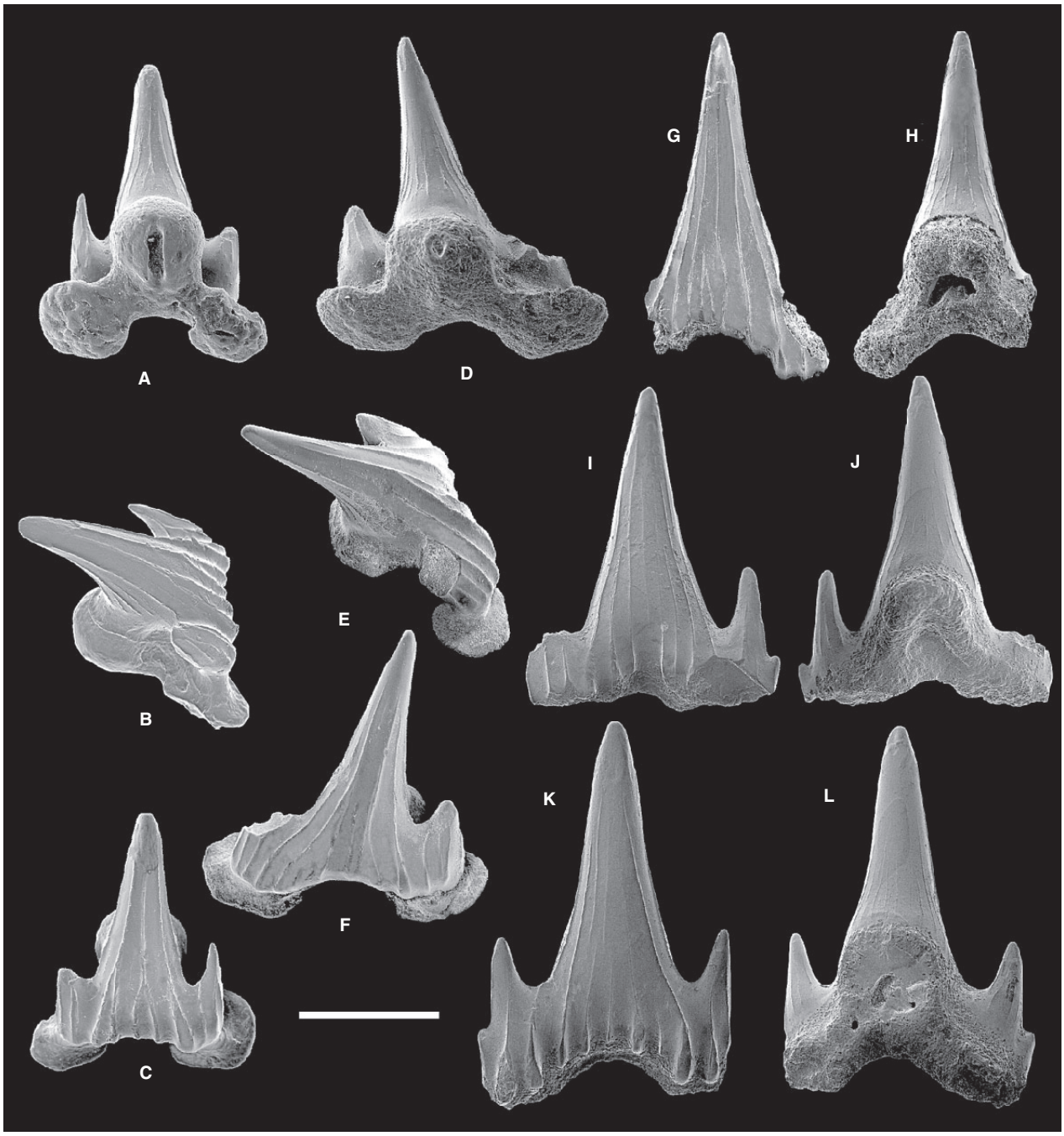
Remarks. The teeth described here are very similar to those of *Palaeoscyllium formosum* from the Kimmeridgian and Tithonian of Germany (Wagner 1857; Leidner and Thies 1999), France (Candoni 1993; as *Parasymbolus octevillensis*) and England (Underwood 2002). They do, however, appear to differ in the possession of a generally finer labial ornament in lateral teeth and the more common occurrence of bifurcation of ridges on the labial face, which is seen only on a small proportion of specimens of *P. formosum*. The higher crown, lack of reticulate labial ornament and more V-shaped root distinguish the Wessex Formation specimens from *P. reticularis* (Underwood and Mitchell 1999). A Valanginian tooth figured by Rees (2005) differs in having more gracile cusps and shorter, non-bifurcating, labial ridges. Despite the differences noted above, which suggest that the Wessex Formation taxon might be specifically distinct, the general similarity of these teeth to those of *P. formosum* and the small number of specimens currently available render specific diagnosis premature.

Palaeoscyllium appears to have been a widespread genus within the northern European Jurassic and Lower Cretaceous, having been recorded from the Bathonian (*P. tenuidens* Underwood and Ward, 2004), Kimmeridgian [e.g. *P. formosum* (Underwood 2002)], Tithonian (e.g. *P. formosum* Wagner, 1857), Valanginian (Rees 2005) and Albian [*P. reticularis* (Underwood and Mitchell 1999); as *Parasymbolus*]. All of these previously described occurrences are from open marine or fully marine lagoonal facies and *Palaeoscyllium* is notably absent in one study of more restricted facies (Underwood 2004). This would appear to be at odds with this new record from the dominantly fluvial Wessex Formation, and would suggest that *Palaeoscyllium* possessed a far greater environmental adaptability than previously realized.

DISCUSSION AND CONCLUSIONS

Palaeoenvironmental occurrence and possible derivation from older strata

The restricted occurrence of neoselachian remains to one bed deposited on a near-coast floodplain (Martill and



TEXT-FIG. 3. Scanning electron micrographs of *Palaeoscyllium* aff. *formosum*. A–C, BMNH P 66293, in: A, lingual view; B, oblique lateral view; C, labial view. D–F, BMNH P 66294, in: D, lingual view; E, oblique lateral view; F, labial view. G–H, BMNH P 66295, in: G, labial view; H, lingual view. I–J, BMNH P 66298, in: I, labial view; J, lingual view. K–L, BMNH P 66299, in: K, labial view; L, lingual view. Scale bar represents 500 μm.

Naish 2001 and references therein) close to the top of the Wessex Formation raises questions concerning uppermost Wessex Formation water salinities. However, despite evidence for slightly raised salinities within some parts of the overlying Cowleaze Chine Member of the Vectis Formation (Radley and Barker 1998), there is, with the possible exception of the neoselachian remains reported here, no evidence for raised salinities in the Wessex Formation (Radley 1994; Radley and Barker 2000). Bed 38 contains a molluscan fauna typical of the Wessex Formation of the Isle of Wight as a whole. This includes unionid bivalves and viviparid gastropods that Radley and Barker (2000,

p. 142) considered to represent 'the best developed freshwater equilibrium fauna of the non-marine Lower Cretaceous of the Weald - Wessex Basin'. In addition, bed 38 contains several other strong indicators of deposition in fresh water including an abundant and diverse lissamphibian fauna, planorbid gastropods and charophytes (SCS, pers. obs.). Bed 38 also contains a large vertebrate fauna of obviously local origin (Radley 1994, pers. comm. 2004). All of the fauna, including the neoselachian reported here, appears therefore to have been resident in the freshwater and terrestrial habitats sampled by the rainstorm-induced floodwaters responsible for the deposition of bed 38 (Insole and Hutt 1994; Haywood *et al.* 2004), and possibly in ponded water existing for some time after the flood waters abated. However, there is a possibility that the neoselachian remains, and perhaps other elements of the microvertebrate fauna, could have been derived from older strata.

In the Isle of Wight, the easternmost of two major *en echelon* basement faults that delineate the northern margin of the Portland-Wight Basin (Underhill 2002), in which the Wessex Formation was deposited, lies less than 1 km north of the outcrop of bed 38. In the Early Cretaceous these faults were extensional in nature, with the uplifted footwall composed of primarily argillaceous strata of Oxfordian and Kimmeridgian age (Radley *et al.* 1998; Underhill 2002). These provided a potential source for reworked Late Jurassic fossils in the Wealden Group. Although derived Jurassic marine macrofossils are frequently encountered at certain horizons in the upper part of the Shepherd's Chine Member of the Vectis Formation at Yaverland (Radley *et al.* 1998), they are extremely rare in the Wessex Formation (Radley 2005). From the southwest coast of the island an ammonite steinkern of Late Jurassic age has been reported by Martill and Barker (2000), and a single, large clast containing Early Jurassic ammonites and other marine fossils has been reported by Radley (1993), but the former is considered to be a regurgitated gastrolith and the latter a dropstone transported in tree roots. Radley (1993, 1994, 2005) also mentioned the occurrence of Portlandian clasts in the Wessex Formation but these are also considered to be either gastroliths or dropstones. Derived Jurassic palynomorphs have been observed (Batten 1996), and Hart *et al.* (1987) recorded calcareous marine nannofossils. However, the small size of these forms, which rendered them easily transported together with the sediments with which they are associated, suggests that they were probably derived from the hinterland rather than locally.

Radley *et al.* (1998) suggested that the occurrence of derived Late Jurassic marine macrofossils in the upper part of the Vectis Formation was linked to wave erosion of the footwall of the basin boundary fault and subsequent dispersal of derived fossils during storm conditions. In Wessex Formation times, the meandering river system gave axial drainage, with probably limited opportunities for footwall erosion and clast transport. Furthermore, much of the higher ground to the north was probably forested (Watson and Alvin 1996), with tree roots aiding soil stability (e.g. Roering *et al.* 2003). The fact that, with the exception of the ammonite steinkern reported by Martill and Barker (2000), no Late Jurassic fossils have been found either in the field or during the sorting of large quantities of residues obtained from bulk screening indicates that animal fossils of Late Jurassic age derived by erosion of the northern margin of the Purbeck-Wight Basin are extremely rare or absent in the Wessex Formation of the Isle of Wight. The unabraded condition of the fragile specimens described here is in marked contrast to the typical preservation of reworked shark teeth elsewhere (e.g. Batchelor and Ward 1990), and this together with the lack of other derived Jurassic fossils in the Wessex Formation argue against them being derived from the Jurassic.

The associated fauna indicates that the Wessex Formation *Palaeoscyllium* was resident in a freshwater environment but teeth of this taxon are rare. Over 550 hybodont teeth were recovered from the samples totalling about 150 kg dry weight taken by us from bed 38 but this sample yielded only three neoselachian teeth. No neoselachian teeth were found in residues from samples totalling more than 2·75 tonnes taken from other beds. This appears to support the conclusion that the Wessex Formation *Palaeoscyllium* may have been a euryhaline neoselachian capable of entering fresh water opportunistically late in Wessex Formation times, possibly at times of flood.

Salinity tolerance in extant neoselachians

Relatively few extant neoselachians enter or live permanently in fresh water, and the majority of those that do are batoids. The Pristidae and Rhinobatidae contain euryhaline species, some of which are known or suspected to breed in fresh water (McEachran 2004*a*, *b*). The Dasyatidae contains species with a range of salinity tolerances, with *Dasyatis* and *Himantura* both containing obligate freshwater, euryhaline and presumed obligate marine species (e.g. Last and Stevens 1994; McEachran 2004*c*). The Potamotrygonidae represents the only extant neoselachian family where all species are obligate freshwater dwellers (Carvalho 2004). The majority of sharks known from fresh water are members of the Carcharhinidae. Species of the poorly known genus *Glyphis* are only known from brackish and freshwater environments (e.g. Last and Stevens 1994). The euryhaline *Carcharhinus leucas* Müller and Henle, 1839, is known to enter fresh water over much of its range, in some areas being commoner in non-marine settings than in the open

sea (e.g. Last and Stevens 1994). An additional carcharhiniforme, *Rhizoprionodon acutus* Rüppell, 1837, has also been recorded in fresh water (Compagno 2004). The only other shark reported to enter fresh water is the orectolobiforme *Chiloscyllium indicum* (Compagno 2001). There are no records of extant members of the Scyliorhinidae in fresh water or even brackish settings, and until this study there was no evidence of scyliorhinid fossils from facies representing these settings. The freshwater occurrence of *Palaeoscyllium* in the Wessex Formation would therefore appear to be unique. Despite this, the freshwater occurrence of a member of an otherwise marine family is typical of modern neoselachians. All of the neoselachian families with extant freshwater taxa, except for the Potamotrygonidae and possibly the Pristidae, contain apparently obligate marine members, with the freshwater occurrences of single species of *Rhizoprionodon* and *Chiloscyllium* being unique within extant members of their families. A freshwater occurrence of these families is currently unknown in the fossil record.

Freshwater neoselachians in the Mesozoic fossil record

Neoselachian remains have been recorded from a number of Jurassic and Early Cretaceous brackish palaeoenvironments, although there is little previous evidence for freshwater forms prior to the Late Cretaceous. A number of neoselachian taxa, including the proscylliid or scyliorhinid *Praeproscyllium* Underwood and Ward, 2004, are known from restricted and presumably somewhat brackish facies in the Middle Jurassic (Underwood 2004). Upper Jurassic (Thies 1995) and basal Cretaceous (Underwood and Rees 2002) brackish facies have yielded teeth of rhinobatid (*s.l.*) rays, but remains of neoselachian sharks have been absent from most samples (but see Rees 2002). A diverse neoselachian fauna reported from the Barremian Wealden of France (Biddle and Landemaine 1988) has been obtained from what appear to be (?transgressive) bonebeds deposited in brackish conditions and not within Wealden facies *s.s.* Albian and later brackish facies have yielded more diverse batoids, including sclerorhynchoids, and some taxa of lamniform shark (e.g. Thurmond 1971). Albian occurrences of lamniform teeth within a supposed fluvial bone bed (Benton *et al.* 2000) suggest that some taxa were capable of entering freshwater lower reaches of rivers on a coastal plain. Neoselachians are known from latest Cretaceous inland freshwater facies (Prasad and Cappetta 1993), these faunas being composed entirely of batoids, including a species of Rajidae, no extant species of which is known from freshwater environments. The presence of teeth of *Palaeoscyllium* in the Barremian Wessex Formation thus represents the earliest known occurrence of a neoselachian within a freshwater environment.

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